## ICP Waters Report 114/2013

Biodiversity in freshwaters: temporal trends and response to water chemistry


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| Title <br> Biodiversity in freshwaters: temporal trends and response to water chemistry | Report No.. 6580-2013 <br> ICP Waters report $114 / 2013$ | Date <br> October 2013 |  |
| :---: | :---: | :---: | :---: |
|  |  | Pages$65$ | Price <br> Free |
|  | $\begin{aligned} & \hline \text { Project No. } \\ & 0-10300 \end{aligned}$ |  |  |
| Author(s) Gaute Velle, Richard J. Telford, Chris Curtis, Lars Eriksson, Arne Fjellheim, Marina Frolova, Jens Fölster, Natalja Grudule, Godtfred A. Halvorsen, Alan Hildrew, Andreas | Topic group <br> Acid deposition, biodiversity | Open |  |
| Hoffmann, Iveta Indriksone, Lenka Kamasová, Jiří Kopáček, Stuart Orton, Pavel Krám, Don T. Monteith, Takaaki Senoo, Ewan M. Shilland, Evžen Stuchlík, Magda-Lena Wiklund, Heleen de Wit, Brit Lisa Skjelkvaale | Geographical area Europe and North America | Printed NIVA |  |


| lient(s) | Client ref. |
| :--- | :--- |
| Norwegian Environmental Agency |  |
| United Nations Economic Commission for Europe (UNECE) |  |


#### Abstract

This report describes trends in biological diversity of benthic invertebrates from acid-sensitive lakes and rivers sampled between 1982 and 2011 in the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The results indicate an overall increase in species diversity during the study period, especially in the rivers. The increase in biodiversity is correlated with declining sulphate concentrations in surface waters, which in their turn are related to reduced atmospheric deposition of sulphur. The changes in biodiversity could be related chemical recovery of surface waters, where reduced sulphate concentrations are associated with increased pH and lowered aluminium concentrations. Apart from the increasing species diversity seen in most sites, the biological recovery trends varied among sites. As a consequence of increased species diversity, the aquatic ecosystems are likely to have a higher resilience against future threats. We can expect an analogous increase in species diversity for comparable sites elsewhere. The improved biodiversity in acid-sensitive waters is in contrast to the world-wide trend of decreasing freshwater species diversity. Our results suggest that international policies to reduce sulphur emissions have promoted a positive development in species diversity of invertebrates in acid-sensitive surface waters.


| 4 keywords, Norwegian | 4 keywords, English |  |  |
| :--- | :--- | :--- | :--- |
| 1. | Sur nedbør | 1. | Acid deposition |
| 2. | Biodiversitet | 2. | Biodiversity |
| 3. | Akvatisk fauna | 3. | Aquatic fauna |
| 4. | Overvåking | 4. | Monitoring |



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# CONVENTION ON LONG-RANGE TRANSBOUNDARY AIR POLLUTION 

INTERNATIONAL COOPERATIVE PROGRAMME ON ASSESSMENT AND MONITORING EFFECTS OF AIR POLLUTION ON RIVERS AND LAKES

## Biodiversity in freshwaters: temporal trends and response to water chemistry

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## Preface

The International Cooperative Programme on Assessment and Monitoring of Rivers and Lakes (ICP Waters) was established under the Executive Body of the UNECE Convention on Long-Range Transboundary Air Pollution (CLRTAP) in July 1985. Since then ICP Waters has been an important contributor to document the effects of implementing the Protocols under the Convention. Numerous assessments, workshops, reports and publications covering the effects of long-range transported air pollution has been published over the years.

The ICP Waters Programme Centre is hosted by the Norwegian Institute for Water Research (NIVA), while the Norwegian Environment Agency leads the programme. A programme subcentre is established at Uni Research, University of Bergen. The Programme Centre's work is supported financially by the Norwegian Environment Agency and by the UNECE LTRAP Trust Fund.

The main aim of the ICP Waters Programme is to assess, on a regional basis, the degree and geographical extent of the impact of atmospheric pollution, in particular acidification, on surface waters. ICP Waters depends on existing monitoring programmes for surface water chemistry and biology in the participating countries. Countries contribute to ICP waters on a voluntarily basis. The ICP site network is geographically extensive and includes long-term data series over 30 years. Over twenty countries in Europe and North America participate on a regular basis. The programme yearly conducts chemical and biological intercalibrations to promote harmonisation and quality assurance of monitoring programmes.

In this report we present an analysis of time trends of biological diversity at the ICP Waters sites and their relation to changes in water chemistry. The biological data set includes about 1.6 million benthic macroinvertebrates sampled from 89 European rivers and lakes collected between 1982 and 2011. In addition, data on water chemistry from the same sites and periods are included. Few, if any, comparable previous studies exist at this scale.

The report was prepared by ICP Waters subcentre in Bergen by lead author Gaute Velle. Most numerical analyses were performed by Richard Telford. Data were provided by those responsible for national monitoring programmes on biota and water chemistry. The results are discussed in several steps with the co-authors.

The report was presented at the Task Force meetings in Pallanza in 2012. We would like to thank all those who contributed with comments to the draft report. We are particularly grateful to all those who collected and contributed monitoring data.

Bergen, October 2013

Gaute Velle
ICP Waters Programme Subcentre

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## Summary

In this ICP Waters report, we provide results from analyses on the species diversity of benthic invertebrates sampled in freshwater monitoring sites from the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The data includes about 1.6 million benthic macroinvertebrates from 5010 samples in 55 rivers and 34 lakes collected between 1982 and 2011. In addition, data on water chemistry from the same sites and periods are included, where such data exist. The study sites were chosen as part of national monitoring programmes and most represent type sites of nutrient poor waters that have been influenced by long-range air pollution leading to acidification. To our knowledge, no comparable studies exist at this scale.

The results from the analysis of water chemistry show that the concentration of sulphate has decreased, while pH and buffering capacity (ANC) have increased. This is in line with previous trend analyses of water chemistry at ICP Waters sites and confirms on-going chemical recovery, as a response to the decrease in long-range transboundary air pollution. Improved chemical status has been associated with a restoring ecological status over the last two decades, as measured by acidification indices. Such acidification indices are based on acid-sensitive taxa in a sample, while the species diversity indices are based on all taxa in a sample. In terms of species diversity, the response will vary according to the initial impact, natural variation and according to biological processes, such as competition and predation. This suggests that acidification indices and species diversity indices are not necessarily correlated, which is confirmed by our results.

According to our results, a majority of the rivers and lakes ( 70 of 89 sites) show a net increase in species diversity (exponential of Shannon's diversity index), albeit the increase is not statistically significant at all sites. This increase is statistically significant for rivers in Germany, Sweden and Latvia. The species diversity of lakes has increased to a smaller extent than the diversity of rivers and only the littoral zone of Swedish lakes shows a significant increase. There was a significant decrease in species diversity in the sublittoral of the Swedish lakes. This decline could be associated with increasing concentrations of dissolved organic carbon (DOC) which result in increases in the colour of lake water. Future records are needed to find whether the non-significant trends can be considered as natural variation or as significant changes. The differences in responses between lakes and rivers could be related to habitat stability where rivers experience more heterogeneous environmental conditions than lakes and lakes therefore are more resilient to changes. This may imply that the biota of rivers is more adapted to a fast re-colonization and that the recovery in the lakes is delayed, or that the biota in the lakes was less influenced by the acidification. In addition, a larger fraction of the taxa are identified to species level in rivers compared to lakes. The implication is that the biota of rivers apparently is more sensitive to changes than the biota of lakes.

The data-analysis suggests that improved species diversity and declining sulphate are correlated. Reductions in sulphate concentrations in acid-sensitive catchments, resulting from reductions in sulphur deposition, are a driver of changes in pH and aluminium, both of which are associated with toxic effects on aquatic biota. In terms of community response, the timing of the recovery and the biological characteristics of the recovery is nonlinear and non-comparable among sites. This suggests that future biological recovery to acidification will not show a universal pattern across sites.

Globally, the species diversity of freshwaters is declining, while the species diversity of the sites in the present study is increasing. Adequate species diversity data on invertebrate populations are lacking from the pre-industrial period and from the period of strongest acidification during the 1970s and 1980s. Documented loss of fish species due to acidification is clear evidence of the loss of biodiversity, and macroinvertebrates may exhibit the same pattern. The improvement of species diversity shown in this report suggests a biological recovery in response to improved water chemistry. We can expect a similar increase in species diversity for comparable acid sensitive waters elsewhere. The biological recovery progress varies among sites, and the strongest recovery probably occurred before monitoring started at some sites, and is still in the initial stages at others. This may explain the lack of significant trends at some sites that have been heavily impacted by acidification, such as in the Czech rivers. The on-going recovery in species diversity recovery indicates dynamic changes in populations and it is unlikely that species diversity is yet back to preindustrial values.

Following increased species diversity, the ecosystems might be expected to be more resistant towards anticipated threats, such as climate change or habitat degradation. It still seems that the species diversity in rivers is more sensitive to changes in environmental conditions than in lakes, highlighting the importance of careful management of rivers.

This international, quality controlled long term monitoring of water chemistry and biota in acidsensitive waters have been important in tracking changes in the diversity of invertebrates in these ecosystems, and their possible causes, i.e. air pollution. Reduction in the emissions of acidifying pollutants has been followed by a positive development in the species diversity of acid-sensitive freshwaters, in sharp contrast to the global trend of decreasing freshwater species diversity.

## 1. Introduction

Pollution that causes acidification has seriously influenced the biota of many European regions. In Norway, detrimental effects on Atlantic salmon (Salmo salar L) and brown trout (Salmo trutta L.) had been reported nearly one century ago (Huitfeldt-Kaas, 1922). Detrimental effects on the most sensitive benthic invertebrates likely began prior to the effects on fish (Raddum et al., 1984). Now, acidifying components in precipitation, surface water chemistry and biota are monitored in international programmes under the Convention on Lon-range Transboundary Air pollution (CLRTAP). Monitoring programmes indicate a reduction in atmospheric pollution since the late 1980's, causing improved water quality and improved ecological state in a broad range of geographical areas (Evans et al., 2001; Halvorsen et al., 2003; Hesthagen et al., 2011; Johnson and Angeler, 2010; Lento et al., 2012; Monteith et al., 2005; Stendera and Johnson, 2008; Stoddard et al., 1999). The biological recovery typically includes reappearance, followed by a modest or pronounced increase in acid-sensitive taxa (Hesthagen et al., 2011; Raddum and Fjellheim, 1995). In this report, we assess for the first time overall trends in biological diversity at monitoring sites since the start of the monitoring. We also assess the influence of water chemistry on the biological diversity.

### 1.1 Biodiversity

Biological diversity, or biodiversity, is a key concept used by scientists, policy makers and laymen. Biodiversity ranges from genetic diversity to the diversity of ecosystems in landscapes (Millennium Ecosystem Assessment 2005; Purvis and Hector, 2000). According to Article 2 of the Convention on Biological Diversity (http://www.cbd.int/convention/articles/default.shtml?a=cbd-02), the term "biodiversity" represents the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

Biodiversity may have important consequences for ecosystem processes, because species types and numbers determine the functional traits in the ecosystem as well as goods and services crucial for human well-being (Chapin Iii et al., 2000; Hooper et al., 2005). Human activities are now responsible for a species loss 100 to 1000 times greater than normal background rates (Rockstrom et al., 2009; UN, 2005). The main causes for the present extinctions include altered land use and over-exploitation of resources, habitat loss and habitat fragmentation, as well as species introduction and pollution. Superimposed on these stressors, climate change now exerts some hitherto uncertain pressure on biodiversity, either directly or indirectly (Heller and Zavaleta, 2009; Mantyka-pringle et al., 2012). As a response to the threats, the partners to the Convention on Biological Diversity committed themselves in 2002 to achieve, by 2010, a significant reduction in the current rate of loss of biodiversity at the global, regional and national level. This target was not met (Spyropoulou et al., 2010) and the loss of biodiversity continues. In October 2010, governments agreed to a Strategic Plan for Biodiversity 2011-2020 aiming at halting and eventually reversing the loss of biodiversity of the planet by 2020. To
build support and momentum for this task, the United Nations General Assembly at its 65th session declared the period 2011-2020 to be "The United Nations Decade on Biodiversity".

### 1.2 Biodiversity in freshwaters

Biodiversity is not evenly distributed among ecosystems. Compared to its volume or surface area, the biodiversity of freshwaters is high compared to the rest of the Earth. Freshwater covers about $0.8 \%$ of the Earth's surface yet includes about $6 \%$ of all described species and $35 \%$ of all vertebrate species (Gleick, 1996; Hawksworth, 1995; Stendera et al., 2012). Freshwater bodies are especially influenced by human perturbations, and freshwaters may be the most endangered ecosystems on Earth (Dudgeon et al., 2006; Sala et al., 2000). Even lakes long considered as pristine sanctuaries at high altitudes- and latitudes are now more or less impacted (Smol et al., 2005). This is alarming since impacted waters are transformed into less desired states that threaten biodiversity and ecosystem services, including supply of water, fishing, recreation and tourism (Scheffer et al., 2001). In North America, it has been estimated that $40 \%$ of all freshwater fish species are at peril (Jelks et al., 2008). The number of unknown species of invertebrates is large and inventories and monitoring programmes of freshwaters are lacking in many parts of the world. The implication is that the number of freshwater invertebrate species that are threatened by extinction is largely unknown. The direct influence of decreasing biodiversity on freshwater ecosystems is still not clear. At least two key influences that affect ecosystem processes can be distinguished: (1) ecosystem resilience may be reduced (Elmqvist et al., 2003), and (2) the rates of ecosystem processes will be modified (Dudgeon et al., 2006; Hooper et al., 2005). A 'healthy' ecosystem can be defined as sustainable system - that is, it has the ability to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience) (Costanza and Mageau, 1999).

### 1.3 Management strategies

The major types of stressors that may combine to affect freshwater ecosystems adversely include overexploitation, (water) pollution, habitat degradation, species invasion and flow modification (Dudgeon et al., 2006). Superimposed on these stressors, climate change exerts an unknown pressure on biodiversity, either directly or indirectly (Currie et al., 2004; Heller and Zavaleta, 2009; Mantykapringle et al., 2012; Mayhew et al., 2012). Responding to the severity of the situation, ecosystem managers facing this "terra incognita" (Steffen et al., 2007) aim at developing management strategies to maintain the goods and services of freshwaters. These management strategies should include assessments of human impact, in order to separate natural phenomena from human-induced influence. At a time of species-loss, in-depth knowledge about biodiversity and its threats is necessary for decisive for successful management.

The threats to freshwaters were especially evident during the second half of the last century, when the influence of acidification caused by long-range transported air pollutants initiated biodiversity loss and alterations of ecosystem processes (Schindler, 1988). Fortunately, management strategies aimed at targeting threats from acid deposition have now caused a reversing trend of the negative impacts for
many sites in Europe and North America. An important part of the policy to combat acid deposition was to establish monitoring programmes, in order to create 'effect-based' policy, i.e. policy to reduce acidifying emissions where it mattered most, based on documented dose-effect relationships. Such monitoring assesses the current condition of ecosystems relative to their past status and has been important in tracking the trajectory of ecosystems and pollution (e.g., Skjelkvaale and de Wit, 2011). With the benefit of hindsight, monitoring should have begun before the onset of anthropogenic acidification, thereby providing indisputable data on pre-disturbance states. In reality, monitoring programmes were initiated only after belated recognition of the effects of acid deposition and rarely started before the 1980 's, i.e., at a time when susceptible waters had already been heavily influenced by acidification. Despite national and international policy implementation to reduce atmospheric acid deposition, evidence of ecological recovery is still equivocal or impeded (Angeler and Johnson, 2012; Lento et al., 2012; Monteith et al., 2005; Murphy et al., in press). The influence on biodiversity and ecosystem function is particularly poorly understood (Johnson and Angeler, 2010; Ledger and Hildrew, 2005) and it is largely unknown whether ecosystem recovery includes a return to a biodiversity and ecological state similar to pre-acidified conditions or to alternate states.

### 1.4 Drivers of biodiversity

A critical issue for lake management is to unravel the factors controlling biodiversity. The main threats to freshwaters, including over-exploitation, water pollution, habitat degradation, species invasion and flow modification, do reduce biodiversity. Apart from perturbations caused by humans, however, patterns of species richness are correlated with latitudinal and other natural gradients (Hawkins et al., 2003; Wright et al., 1993). Rohde (1999) concluded that latitudinal gradients in species diversity result from effective evolutionary time modulated by several factors, such as temperature and energy input. At a smaller scale, factors controlling biodiversity include interactions among many abiotic and biotic variables, such as disturbance and stream stability, eutrophication, food availability and available area (Lods-Crozet et al., 2001; Solimini et al., 2008; Stendera et al., 2012). For aquatic insects, species richness and assemblage composition are also strongly correlated with habitat size and acidity (Heino, 2009). The relationship between species richness and acidity also implies that biodiversity can be expected to increase as atmospheric pollution is reduced.

### 1.5 Measuring biodiversity

An ideal biodiversity index is able to reduce complex information on structure and abundance to simple numerical metrics. However, it is important to be aware of two main limitations to the concept of biodiversity: (1) the term is artificial implying that biodiversity not is an intrinsic property in nature and (2) biodiversity is a simplification of nature and it is necessary to consider that information is lost when complex processes are reduced to a single number (Hurlbert, 1971). Since biodiversity has many meanings and is generally poorly understood, the term is inevitably used inconsistently and often imprecisely. In order to avoid misunderstandings, here we restrict ourselves to species diversity - a major component of biodiversity and with a clear scientific definition.

In his development of a conceptual family of species diversity indices, Whittaker (1960) determined the total diversity in the landscape ( $\gamma$-diversity) by the diversity at one site ( $\alpha$-diversity) and the diversity difference among sites or with time ( $\beta$-diversity). For the basic unit of biological classification, the species, $\alpha$-diversity is expressed as a function of the number of species and their frequency (Chapin Iii et al., 2000; Tuomisto, 2010). The present study focuses on $\alpha$-diversity and $\beta$ diversity. In addition to the conceptual family, another family of biodiversity indices include so-called functional diversity metrics. Functional diversity reflects the biological complexity of the ecosystem expressed by important biological traits (Heino, 2005, 2008; Schleuter et al., 2010). Such traits could include feeding mode, food source, mode of mobility, size at maturity, life cycle length etc. A change in these traits over space or time gives direct information about ecological processes

Several indices exist for measuring $\alpha$-diversity, each with its own set of limitations and advantages. All indices also come with a set of assumptions. These assumptions should aid in the selection of species diversity index according to the data at hand, so that they are violated as little as possible. The indices weight the number of species and their frequency differently, but most are correlated within a given community (DeBenedictis, 1973). The most basic diversity metric is based solely on the total number of species collected (species richness). Although richness is an intuitive measure of species diversity, being easy to understand, many ecologists prefer to avoid using it for a number of reasons. Species richness is correlated with the sampling effort in the field (Bady et al., 2005; Jost, 2006; Lande, 1996), so sampling effort should be standardized before richness can be compared within sites or among sites. Common and rare taxa are given equal weight in species richness, which gives dubious ecological meaning and also leads to a measure of species diversity that is slow to converge to a definite value. Consequently, repeated samples from an ecosystem often show a high variability in species richness compared to other indices of species diversity.

Researchers have pointed out that estimation of species diversity not is straightforward because of bias due to varying sample size (Birks and Line, 1992) and suggest that rarefaction analyses should be used when assessing it. In rarefaction, the sample size is standardized by weighting the contribution of each species by its abundance or occurrence (Birks and Line, 1992; Walker et al., 2008). Estimation of species richness by rarefaction has many advantages. However, rarefaction assumes that the number of occurrences of a species reflects the sampling intensity, implying that rarefaction curves will be skewed if the sampling effort is not comparable among sites. Also, rarefaction is problematic if some of the samples are very small.

Most other diversity-indices, such as the Simpson, Shannon, or Berger-Parker indices include species proportions or frequencies in their calculation. The advantage is that common and rare taxa have unequal weight, so that biological communities are differentiated more effectively. The weighting differs among indices, where some weigh common taxa, while others weight rare taxa. Compared to species richness, such indices may at first sight seem difficult to interpret. However, this is overcome by converting the indices into effective number of species measured in species units. The effective
number of species is the number of equally-common species required to give a particular value of the index (Jost, 2006).

### 1.6 Aims of study

In the present study, we have used extensive monitoring data on benthic macroinvertebrates (Figure 1) and water chemistry sampled from mid-1980 and up to the present. Participating countries in this study include the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. Importantly, all countries participate in both hydrochemical and macroivertebrate intercomparison schemes that ensure international comparability.

Our primary objectives have been to use robust numerical techniques and a suitable measure of biodiversity for the data at hand to (1) record trends in the species diversity of benthic macroinvertebrates from the beginning of the monitoring period to the present, (2) search for common trends in $\alpha$-diversity among sites, (3) examine $\alpha$-diversity in the light of the external chemical stressors, especially chemical variables related to acidification and (4) search for common community changes among sites (temporal $\beta$-diversity). In future studies, we hope to also focus on the influence of temperature on $\alpha$-diversity, to analyse the functional diversity of communities and to model $\alpha$ diversity as a function of future scenarios of temperature and water chemistry.


Figure 1. Benthic invertebrates from Norwegian rivers. From left to right the stonefly Diura nanseni, the caddisfly Potamophylax sp. and the mayfly Baetis rhodani. Photos by A. Fjellheim (Uni Research).

## 2. Methods

### 2.1 Study sites

Study sites include lakes and rivers from the Czech Republic, Germany, Latvia, Norway, Sweden and UK (Table 1 and Table 2, APPENDIX A - Study sites). The full data set includes about 1.6 million benthic macroinvertebrates from 5010 samples in 55 rivers and 34 lakes collected between 1982 and 2011 (Figures 1-3, Tables 1-2). These sites form part of national biological- and chemical monitoring programmes in running and standing freshwaters (Halvorsen et al., 2002; Horecký et al., 2002; Horecký et al., 2006; Horecký et al., 2013; Johnson and Goedkoop, 2007; Kernan et al., 2010; Schaumburg et al., 2008). The bedrock varies among sampling regions, but apart from Latvia, most sites are in acid-sensitive bedrock consisting of gneiss, granite or quartzite. The Latvian sites are situated on claystone including smaller fractions of dolomite and gypsum. In terms of vegetation, the northernmost sites are situated in boreal vegetation and the southernmost sites are situated in cool temperate vegetation. Some of the sites, especially in Germany and Latvia, are placed in small stands of forest surrounded by farmland. In addition to biological samples, the data include water chemistry measurements. A combined data set was compiled that includes paired invertebrate samples and chemistry samples (Table 1 and Table 2).

Table 1. Samples from rivers with number of biological samples, number of sub-samples, average sample size, number of paired chemistry samples and sampling period. All biological samples have been taken by kicksampling. *The Norwegian rivers include a total of 59 sampling stations.

|  | Number <br> of Rivers | Biological <br> samples | Sub- <br> samples | Average <br> sample size | Chemical <br> samples | Sampling <br> period |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Czech Republic | 4 | 58 | 1 | 1102 | 57 | $1999-2011$ |
| Germany | 29 | 1074 | 1 |  | 1074 | $1982-2010$ |
| Latvia | 5 | 46 | 1 | 150 | 38 | $1997-2011$ |
| Norway | $3^{*}$ | 2255 | 1 | 217 | 284 | $1987-2010$ |
| Sweden | 6 | 91 | 5 or 6 | 236 | 91 | $1985-2011$ |
| UK | 11 | 234 | 3 or 5 | 1312 | 216 | $1988-2010$ |

Table 2. Samples from lakes with number of biological samples, number of sub-samples, average sample size, number of paired chemistry samples and sampling period. Note that the Swedish littoral, sublittoral and profundal samples were taken from the same seven lakes. Grab samples were taken by use of an Ekman grab.

|  | Lakes | Biological <br> samples | Sub- <br> samples | Sampling <br> method | Average <br> sample size | Chemical <br> samples | Sampling <br> period |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Norway | 20 | 558 | 1 | Kick | 282 | 378 | $1997-2010$ |
| Sweden littoral | 7 | 179 | 5 | Kick | 195 | 179 | $1986-2010$ |
| Sweden sublittoral | 7 | 155 | 5 | Grab | 227 | 155 | $1989-2010$ |
| Sweden profundal | 7 | 228 | 5 | Grab | 183 | 195 | $1986-2010$ |
| UK | 6 | 132 | $3-7$ | Kick | 442 | 130 | $1988-2010$ |



Figure 2. Sampling sites. Red dots denote running waters and blue dots denote standing waters. There are a total of 112 sampling sites in rivers and 48 sampling sites in lakes.


Figure 3. Sampling in the upper reaches of River Gaular in Norway. This site is typical for the Norwegian rivers. Photo by P. Fagard (Uni Research).

Water chemistry was sampled at the biological sampling stations, but not at every sampling station and not for all corresponding sampling-times. As criteria for the inclusion of water samples, the samples should be from the biological sampling stations and be sampled not more than two weeks after, or six weeks before, the time of biology sampling. The time window was skewed towards chemistry samples preceding the biological sampling assuming that the assemblages had indeed experienced past chemistry, but that the influence of an unknown future chemistry was uncertain. For the same reason, when more than one chemistry sampling date could be paired with a biological sample, the date preceding the time of the invertebrate sampling was preferred. The combined data set includes 2797 samples with about 950000 benthic invertebrates and about 35000 data entries on water chemistry. Chemical variables includes pH , conductivity, alkalinity, calcium (Ca2+), magnesium (Mg2+), potassium $(\mathrm{K}+)$, sodium $(\mathrm{Na}+$ ), chloride ( $\mathrm{Cl}-)$, sulphate (SO42-), total nitrogen (TotN), nitrate (NO3-), total organic carbon (TOC), hydrogen ( $\mathrm{H}+$ ) and labile aluminium (LAL). Acid-neutralizing capacity (ANC) was calculated as $(\mathrm{Ca}+\mathrm{Mg}+\mathrm{Na}+\mathrm{K}+\mathrm{NH} 4)-(\mathrm{Cl}+\mathrm{SO} 4+\mathrm{NO} 3)$. For a detailed description of measured water chemistry, see Skjelkvaale and de Wit (2011). For a full list of sites, including name, geographical coordinates, altitude, lake depth, lake area, number of biological samples, number of chemical samples and sampling period, see APPENDIX A - Study sites.

### 2.2 Sampling and species identifications

Most invertebrates were collected by kick sampling (Frost et al., 1971), following the ICP-Waters manual (Wathne et al., 2010). In this procedure, the substrate is disturbed and collected in a 0.25 mm mesh net (Figure 4). An Ekman grab was used in the Swedish sublittoral- and profundal lake sites. The sampling interval varied among sites and years with an average of about 1.5 samples per sampling station per year from the time most monitoring programmes opened in 1987 and up to the present.


Figure 4. Kick-sampling for benthic invertebrates in a Norwegian river. Photo by G.Velle (Uni Research).

Each sample was sorted under a stereo microscope in the laboratory, and macroinvertebrates subsequently identified. Leeches (Hirudinea), molluscs (Mollusca), mayflies (Ephemeroptera), stoneflies (Plecoptera), caddis flies (Trichoptera), water beetles (Coleoptera), dragon flies (Odonata) and water bugs (Hemiptera) were identified to the lowest possible taxon, i.e. species or genus, whereas most other taxa were identified to family or genus. The zoobenthos were identified with the use of extensive national and international keys, such as Askew (1988), Lillehammer (1988), Nilsson (1996) and Wallace et al. (1990).

### 2.3 Consistency in taxonomic resolution and sampling season

The specimens were identified by local experts and the data are of high quality. The data contributors have also participated in annual ICP-waters biological- and chemical inter-calibrations (e.g., Dahl and Hagebø, 2011; Fjellheim et al., 2011; Raddum, 1993). The inter-calibration focuses on improving the quality of work at the national laboratories as well as harmonisation of methods and databases. The biological inter-calibration focusses on the taxonomic skills of the participants and each participating laboratory identifies mixed samples of invertebrates. Based on the fraction of specimens correctly
identified to genus or species, and on the fraction of specimen identified, the laboratory is given a quality assurance index. A score above 80 is regarded as good. The score was around 80 during the first years of the inter-calibrations and has now stabilized at about 95 (e.g., Fjellheim et al., 2011; Raddum, 1993), indicating taxonomic excellence.

Despite a standardized sampling procedure and high taxonomic accuracy, it remains possible that taxonomic resolution has varied over the last 30 years of monitoring. Since we are analysing trends in species diversity over time and not comparing the absolute diversity among sites, taxonomic resolution does not need to be standardized among sites. However, if the taxonomic resolution has varied systematically at any one site, then the trends in species diversity may be biased. Inevitably, many taxa are sometimes identified to species and other times to a broader taxonomic level. Such inconsistencies could be caused by varying larval size at the time of sampling where small specimens cannot be identified to species. In order to test for systematic inconsistencies, we first registered the lowest taxonomic level that supra-specific taxa were identified to. Then, in a second step, we plotted the fraction of specimens identified to the lowest taxonomic level (usually species) in each sample against time. For taxa that sometimes are identified to species and sometimes to a broader taxonomic resolution, there should not be a relationship between taxonomic resolution and time. In order to correct for inconsistencies, the taxonomy was amended to a broader level by merging taxa with inconsistency taxonomy until any trend in taxonomic resolution disappeared.

Time of sampling during the year may also influence species diversity. A great number of taxa are usually found during autumn than during spring. Consistent sampling will not compromise diversity (e.g., samples are collected in spring and autumn every year). However, inconsistent changes in sampling season, e.g., a change from all autumn sampling to all spring sampling, may cause changes in diversity. In order to detect any inconsistency in time of sampling, the sampling quarter was recorded for all samples at any one site and plotted against time and against diversity.

### 2.4 Numerical analyses

As a measure of $\alpha$-diversity, we have adopted the exponential (exp) of the Shannon entropy (N1). The mathematical formula for N 1 is used in information statistics as a general measure of uncertainty and diversity. When used as an index of species diversity, it translates into effective number of species measured in species units. The exponential of N 1 is then calculated as:
$\mathrm{N} 1=\exp \left(-\sum_{i=1}^{s} p_{i} \ln p_{i}\right)$
where p is the relative abundance of taxon i in the sample and ln is the natural logarithm. N 1 is comparable among unequal-sized communities since it converges quickly to a stable value, weighs all species in proportion to their frequency in the sample and is weakly influences by common or rare species (Jost, 2006). N1 assumes that all individuals are sampled randomly, that the population is indefinitely large (effectively infinite) and that all species in the community are represented. It may be
difficult to justify these assumptions for many communities, particularly very diverse communities. Moreover, the assumptions indicate that incomplete sampling may cause bias. Nevertheless, we still assume that any abs caused by potential violations of the assumptions are slight and that this is the most appropriate index to use in the present study. The sample size in the study varies by three orders of magnitude, implying that rarefaction is not feasible.

Linear trends in diversity for each site and for each country were assessed by use of linear mixed effect models (lme) with random intercept and slope, and tested for statistical significance. The species diversity trends (negative or positive) from a linear least squares model for each site were also plotted on a map. Non-linear methods (generalized additive models, GAM) were used for sites that included more than ten samples. The number of degrees of freedom in GAM was set to ten.

As a measure of the difference in community composition over time at any one site ( $\beta$-diversity), we have used non metric multidimensional scaling (NMDS). NMDS is an ordination technique that visualizes the level of similarity among species assemblages. Unlike other ordination methods, NMDS makes few assumptions about the nature of the data, e.g. about linearity or unimodality. In a NMDS diagram, proximity reflects similarity in species composition among samples. We used Bray-Curtis as a distance metric.

The influence of chemical variables on species diversity (N1) was also tested. In such an analysis, it is not straightforward to run the full dataset into one joint analysis, i.e., as a multiple regression with water chemistry as independent variable and species diversity as dependent variable. The range in any environmental variable of interest varies among sites where both high and low values may be associated with high and low diversity. Further, the biological sensitivity to acidification varies among regions of Europe (Raddum and Skjelkvale, 2001), also for single species (Moe et al., 2010), suggesting site-specific analysis. Hence, we have assessed the relationship at each site independently and summed up the overall findings. The correlation was assessed by use of lme and tested for statistical significance. Significance was corrected for multiple tests with Bonferroni correction. Many of the chemical variables, such as some major ions, are closely correlated with one another, and some chemical variables are derivatives of others. In addition, not all chemical variables were measured at every site. In order to reduce collinearity and noise, only six chemical variables ( $\mathrm{pH}, \mathrm{SO} 4, \mathrm{NO} 3, \mathrm{NH} 4$, ANC and conductivity) were retained in the analyses.

All numerical analyses were performed using the statistical package $R$ ( R development core team 2010) using several statistical libraries (RODBC, vegan, maps, mapdata, mgsv, MASS and nlme).

## 3. Results

### 3.1 Consistency in taxonomic resolution and sampling season

For several regions, the fraction of the zoobenthos identified to species compared to that resolved more coarsely has changed considerably since monitoring began (Figures 5 and 6, Table 3). This altered taxonomic resolution is most pronounced in the German streams, in the Norwegian rivers, in the Czech inflow streams, in the sublittoral of Swedish lakes and in UK lakes. For these sites, uncorrected trends in species diversity can be expected to be more or less biased.

Table 3. The correlation (linear or non-linear, whichever is highest) between taxonomic resolution and time for the original data and in the amended data subsequent to taxonomic correction. Trends in this relationship can lead to biased species diversity measures. In order to remove this potential bias, taxa in the original dataset were merged until the correlation between taxonomic resolution and time in the amended dataset was close to zero. Only taxa that influenced $\mathrm{R}^{2}$ were merged. For a complete list of merged taxa, see APPENDIX B - Taxonomic consistency. * indicates significance at $\mathrm{p}<0.05$.

|  |  | Taxonomic resolution versus time $\left(R^{2}\right)$ |  |
| :--- | :--- | :--- | :--- |
|  | Country | Original dataset | Amended dataset |
| Streams | Czech Republic | $0.5^{*}$ | 0.001 |
|  | Germany | $0.081^{*}$ | 0.006 |
|  | Sweden | $0.041^{*}$ | 0.006 |
|  | UK | 0.002 | 0.002 |
|  | Latvia | 0.05 | 0.005 |
|  | Norway: Vikedal | 0.027 | 0.027 |
|  | Norway: Gaula | 0.041 | 0.022 |
|  | Lakesway: Nausta | 0.031 | 0.031 |
|  | Norway | 0.041 | 0.007 |
|  | Sweden: littoral | $0.260^{*}$ | 0.06 |
|  | Sweden: sublittoral | $0.093^{*}$ | 0.016 |
|  | Sweden: profundal | 0.015 | 0.015 |
|  | UK | $0.232^{*}$ | 0.026 |
| Average |  | $0.1^{*}$ | 0.017 |



Figure 5. Biological samples from rivers with potential sources of biased species diversity estimates, including consistency in sampling season and taxonomic resolution over time. The number of samples (left-hand scale) is shown as bars and indicates the quarter of sampling (Q1-Q4) during the year. The grey line indicates the taxonomic resolution (right-hand scale) in each study region based on the raw biological data. The taxonomic resolution is the average fraction of specimens identified to the lowest taxonomic level (usually species) in each country (absolute numbers are not comparable among sites). Only taxa that sometimes were identified to species and sometimes to a coarser taxonomic level were included. In an amended dataset, such taxa were merged to a coarser unit so that the relative taxonomic resolution became a horizontal line (Table 3, see also APPENDIX B Taxonomic consistency).


Figure 6. Biological samples from lakes with potential sources of biased species diversity estimates, including consistency in sampling season and taxonomic resolution over time. The number of samples (left-hand scale) is shown as bars and indicates the quarter of sampling (Q1-Q4) during the year. The grey line indicates the taxonomic resolution (right-hand scale) in each study region based on the raw biological data. The taxonomic resolution is the average fraction of specimens identified to the lowest taxonomic level (usually species) in each country (absolute numbers are not comparable among sites). Only taxa that sometimes were identified to species and sometimes to a coarser taxonomic level were included. In an amended dataset, such taxa were merged to a coarser unit so that the relative taxonomic resolution became a horizontal line (Table 3, see also APPENDIX B Taxonomic consistency).

In general, the taxonomic resolution has remained stable or increased since 2000-2002, consistent with the enhanced focus on taxonomic harmonization procedures and taxonomic skills among members of ICP Waters. Since that time, inter-calibration was performed annually. Data from sites with inconsistent taxonomic resolution were reduced to a coarser taxonomic level prior to numerical analysis (Table 3). We only present diversity results from the corrected dataset.

The number of samples acquired during any one year can be seen from Figures 5 and 6. Some regions show a decreasing number of samples towards the present, e.g., in rivers from Norway, Germany and the UK, and in lakes from UK. Reduced funding has caused this decline.

With regard to sampling season, most regions are sampled consistently in spring (UK), in spring and autumn (Norway), or at a higher frequency (Czech Republic, Latvia and Germany). There was a shift from spring to autumn sampling for Swedish rivers and lakes in the mid-1990s (Figures 5 and 6).


Figure 7. Boxplot showing overall trends in species diversity for all rivers and lakes. The box marks the 25th and 75th percentile and the median, the whiskers mark the interquartile range and the circles denote outliers. The width of the box indicates the number of samples. Values above the zero line denote an increase in diversity and values below zero denote a decrease in diversity. Statistically significant trends at the national level are marked with *, where ${ }^{*} \mathrm{p}<0.05$ and ${ }^{* * *} \mathrm{p}<0.001$.

### 3.2 Temporal trends in species diversity ( $\alpha$ - diversity)

Most regions have shown some increase in $\alpha$ - diversity over the last 25 years (Figure 7). Diversity has increased significantly in the German rivers, Swedish rivers, Latvian rivers and in the littoral of Swedish lakes (Figures 9 and 10). There has been a significant decrease in species diversity in the sublittoral of Swedish lakes. Overall, it seems that the increase in diversity is more pronounced for rivers than for lakes. Non-linear trends for sites with a significant change in diversity are shown in Figure 10, while raw data and non-linear trends for all sites can be found in APPENDIX C - diversity details. There is no clear influence of altered sampling season on the species diversity of the Swedish lakes, while the Swedish rivers show a break point concurring with the shift. Still, it seems this break point does not alter the diversity trend since there was an increase before and after the shift.


Figure 8. Species diversity (Shannon $\mathrm{N} 1_{\exp }$ ) for zoobenthos in rivers from The Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The blue lines represent the signal in single rivers (measured by linear mixed effect models), whereas the red line represents the overall signal for each country. * denotes the significance level of the diversity change, where * $\mathrm{p}<0.05$ and $* * * \mathrm{p}<0.001$.


Figure 9. Species diversity (Shannon $N 1_{\text {exp }}$ ) for zoobenthos in lakes from Sweden, Norway and the UK. The blue lines represent the signal in single lakes (measured by lme), whereas the red line represents the overall signal for each country. * denotes the significance level of the diversity change, where * $\mathrm{p}<0.05$ and ${ }^{* * *} \mathrm{p}<$ 0.001 . The Swedish littoral, sublittoral and profundal samples were taken from the same lakes.

### 3.3 Assemblage changes over time ( $\boldsymbol{\beta}$-diversity)

The biological assemblages show little consistent patterns of change over time and much intern-annual variability, with the exception of the littoral in Swedish lakes (Figure 11). Here, the assemblages have changed consistently since the 1980s and towards the present. This implies that most sub-littoral Swedish taxa have undergone similar changes at all sites, e.g., either decreasing or increasing abundance. The Swedish sublittoral assemblages show some directional changes, but not as clear as the littoral samples. There are no clear changes in the profundal of the Swedish lakes or for any other datasets. For these sites, the NMDS indicates that the taxa composition may have changed, but not in unison and not to any new states. The assemblages are more or less the same now as they were in the 80s or 90s.


Figure 10. Non-linear (GAM) curve-fits of species diversity (Shannon $\mathrm{N} 1_{\exp }$ ) for regions with a statistical significant change in diversity. For all regions, see APPENDIX C - diversity details.


Figure 11. $\beta$-diversity analysed by non-metric multidimensional scaling (NMDS) in selected countries. The trajectories (lines) show assemblage changes from the 1980s and towards the present with colour codes representing decade of sampling. Closely placed samples have a similar species composition. Only the littoral of Swedish lakes show directional patterns of change, whereas for the other regions, the assemblages change seemingly at random. For missing plots, see APPENDIX C - diversity details.

### 3.4 Relationships between water chemistry and species diversity

A chemical recovery was evident in the study sites. The most pronounced changes include decreased concentration of SO4 (sulphate), increased pH and increased ANC (Figure 12 and 13). For Latvia, pH has remained stable. The Latvian sites are situated on limestone and have not experienced acidification. For these sites, the reduction in SO4 is unlikely to be related to a reduced sulphate deposition, because deposition adds only a fraction to the background sulphate from the bedrock. Probably, some other factors play a role, such as climate, drought or agriculture.

Sulphate is the most pronounced chemical cue related to species diversity in the rivers as there is a statistically significant negative correlation between diversity and sulphate in 17 of 61 sites. (Figure 12, Table 4). Eleven of the rivers show a positive correlation between ANC and diversity. The relationship in lakes is noisy where a chemical parameter seemingly can influence diversity positively and negatively (Table 5), suggesting it is not causational. For example, there is a positive correlation between sulphate and diversity for three sites and a negative correlation for five sites.


Figure 12. An example on the relationship (based on linear mixed effect models) between water chemistry and species diversity ( N 1 exp ) for rivers in Norway. Red lines denote significant trends ( $\mathrm{p}<0.05$ ). See Table 4 and Table 5 for the relationship elsewhere.

Table 4. Number of sites with a significant correlation between species diversity ( $\mathrm{N} 1_{\exp }$ ) and measured water chemistry variables in rivers. The correlations are either positive or negative in the table (positive/negative). n denotes number of sites where both biological and chemical data are present, ANC denotes acid neutralizing capacity and NA denotes that chemical data is not available.

| RIVERS | n | pH | ANC | $\mathrm{SO}_{4}$ | $\mathrm{NO}_{3}$ | $\mathrm{NH}_{4}$ | Conductivity |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Czech Republic | 4 | - | $1 / 0$ | $0 / 1$ | $0 / 1$ | - | $0 / 1$ |
| Germany | 29 | $5 / 0$ | $5 / 0$ | $0 / 9$ | $0 / 8$ | $0 / 2$ | NA |
| Latvia | 2 | - | $1 / 0$ | $0 / 2$ | - | - | - |
| Norway | 9 | $3 / 0$ | $2 / 0$ | $0 / 3$ | $0 / 2$ | NA | - |
| Sweden | 6 | $0 / 1$ | $2 / 0$ | $0 / 2$ | - | - | $0 / 1$ |
| UK | 11 | $1 / 0$ | - | - | - | NA | $2 / 0$ |
| Total | 61 | $9 / 1$ | $11 / 0$ | $0 / 17$ | $0 / 11$ | $0 / 2$ | $2 / 2$ |

Table 5. Number of sites with a significant correlation between species diversity ( $\mathrm{N} 1_{\exp }$ ) and measured water chemistry variables in lakes. The correlations are either positive or negative in the table (positive/negative). n denotes number of sites where both biological and chemical data are present, ANC denotes acid neutralizing capacity and NA denotes that chemical data is not available.

| LAKES | n | pH | ANC | $\mathrm{SO}_{4}$ | $\mathrm{NO}_{3}$ | $\mathrm{NH}_{4}$ | Conductivity |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Norway | 20 | $0 / 1$ | $0 / 1$ | $1 / 0$ | $1 / 3$ | NA | $1 / 0$ |
| Sweden litt. | 7 | $2 / 0$ | $4 / 0$ | $0 / 4$ | $0 / 2$ | - | $0 / 2$ |
| Sweden sublitt. | 7 | $0 / 1$ | $0 / 3$ | $1 / 0$ | $1 / 0$ | - | $3 / 0$ |
| Sweden prof. | 7 | $0 / 1$ | $0 / 1$ | - | $1 / 0$ | $1 / 1$ | $1 / 1$ |
| UK | 6 | $1 / 0$ | - | $1 / 1$ | - | NA | $0 / 1$ |
| Total | 47 | $1 / 3$ | $4 / 5$ | $3 / 5$ | $3 / 5$ | $1 / 1$ | $5 / 4$ |



Figure 13. Boxplots showing change per year in $\mathrm{pH}, \mathrm{SO}_{4}$ and ANC during the water sampling periods covered by the different regions. Numbers along the base indicate the chemistry mean measurement for each country during the full sampling period. Note that measurements from the Swedish lake littoral-, sublittoral- and profundal samples indicated similar results and were lumped in the figure.

## 4. Discussion

### 4.1 Taxonomic resolution

In German rivers, Norwegian lakes and the sublittoral of Swedish lakes, taxonomic resolution increased steadily over the first years of the biological monitoring and then reached a plateau at which it has remained (Figures 5 and 6). This development is expected as the taxonomists steadily increased their skills. For the biological assemblages from the Norwegian rivers, Czech rivers, Swedish rivers and the UK lakes, the taxonomic resolution shows a pronounced U-shape with decreasing taxonomic resolution during the first years followed by an increasing trend towards the present. The decreasing resolution after the commencement of the sampling programmes is somewhat surprising. It may be that the decrease was caused by a monitoring focus on acid-sensitive indicator taxa and less focus on the full assemblage. After all, the programmes commenced in order to monitor the influence of acidification and not to capture the full biological communities. Then, as new biological acidification indices emerged (e.g., Moe et al., 2010), the list of acid-sensitive taxa expanded, leading to an increased taxonomic resolution.

By merging taxa and correcting for inconsistent taxonomic resolution, the data sensitivity may be coarser. However, without correction, the observed increase in $\alpha$ - diversity may partly or fully be attributed to the increased taxonomic resolution. For example, the diversity increase is statistically significant in the Norwegian lakes- and rivers prior to the taxonomic correction and not significant subsequent to the correction. Also, the diversity of the Swedish sublittoral was not significant prior to the correction and significant subsequent to the correction. The correction may explain possible discrepancies between our results and results from previous national studies.

The results highlight the importance of thoroughly testing for taxonomic consistency when studying long biological records from species data. Typically, multiple taxonomists have been involved over the years. The focus on biological groups may have changed according to the research question being asked at the time of sampling and according to taxonomic expertize. The skills of benthic invertebrate taxonomists are highly specialized and few can identify all groups. It is also clear that the taxonomic resolution may vary according to age of the specimen, since small stages are often hard to identify. Inevitably, some specimens in a sample cannot be identified reliably. Most larvae are typically small during summer and early autumn, but the larval size may also vary with food availability and temperature. Nevertheless, the fraction of unidentifiable larvae should be fairly stable over time and not influence the taxonomic consistency significantly, assuming there were no changes in seasonal sampling.

The altered taxonomic consistency also highlights the importance of performing internal standardization procedures and inter-calibration in biological inventories (e.g., Fjellheim et al., 2011). Biomonitoring is time-consuming and economically expensive. Society and research communities will
benefit if the data can be exploited fully, including for purpose other than those of the original exercise. At the same time, the value of the data depends on their quality.


Figure 14. Trends in $\alpha$ - diversity (effective number of species, $\mathrm{N} 1_{\mathrm{exp}}$ ) for zoobenthos in all rivers and lakes in the study. The linear trends are from a least squares model where + indicates an overall increase since the start of the site- specific sampling programme and - denotes a decrease. For the Norwegian rivers, note that not all trends are statistically significant (for significant trends, see Figures 8 and 9).

### 4.2 Temporal trends in species diversity ( $\alpha$ - diversity)

A biological response to altered environmental conditions, such as the amelioration of acidification, will include at least one of three phenomena (modified from Guisan, 1995; Hengeveld, 1990): (1) unknown primary and secondary effects on the species and on the ecosystem, (2) biological migration such as a shift in ranges and (3) species extinction. Most, but not all sites, show an increased species diversity (Figure 14), even in a time of decreasing acidification and improved biological acidification indices. The recovery in terms of species diversity depends on the initial response to the acidification. For sites that were strongly acidified, e.g. in Germany and the Czech Republic, the recovery is expected to result in a significant increase in diversity. Such a recovery is seen for the German rivers
as a highly significant increase in species diversity. The diversity of three Czech rivers is increasing, albeit, not significantly since the diversity of Litavka River is decreasing. Litavka is the most acidified site of the Czech rivers (Horecký et al., 2006) and may a need as much as 50 years to recover (Hardekopf et al., 2008). The zoobenthos of Litavka is influenced by regular droughts during the summer (Horecký et al., 2013), however the decreasing diversity at this site (Figure 8) is most likely caused by the intensive forest clearings during the last two years of sampling. Notably, the forest clearing significantly influenced the water channel and damaged the river habitats and at the same time contributed to the both a chemical and a biological recovery in the stream (Stuchlík, personal observation), demonstrating the complexity of the recovery process. It is also important to consider that not all sites would be expected to show an increase in species diversity consequent upon chemical recovery. For example, the pre-disturbance community may have consisted of insensitive taxa, or the acidification eradicated fish populations (Hesthagen, 1986), allowing invertebrates that are sensitive to fish predation to flourish (Appelberg et al., 1993; Hildrew, 2009; Layer et al., 2011).

Interestingly, trends in the biota of the Swedish lakes depend on the habitat sampled. There has been a significant increase in the littoral, a significant decrease in the sublittoral, and no changes in the profundal. Environmental conditions in the shallow littoral fluctuate daily and/or seasonally, whereas the conditions are stable in the profundal. Such conditions include temperature, dissolved oxygen (DO), discharge from streams and abundance of macrophytes. All zones have experienced a similar recovery from acidification. However, the fauna of the profundal experiences more stable conditions and is less affected by the environmental changes that may accompany the recovery. DO may be a limiting factor in the profundal such that the influence from acidification is less pronounced.

When it comes to the divergent signals from the littoral sublittoral, it is interesting to note that the dissolved organic carbon (DOC) has increased significantly in these lakes during the last 25 years (data not shown, see also Monteith et al., 2007; Skjelkvåle et al., 1999). Such an increase in DOC has been observed in many regions and it has been suggested that the increase is linked to warmer conditions (Freeman et al., 2001) or to declining deposition of sulphur and sea salt (Monteith et al., 2007). DOC and water colour are generally correlated (Schindler et al., 1996; Wallage and Holden, 2010), suggesting that the depth of the photic zone, within which levels of light are sufficient to support the growth of aquatic macrophytes and algae, will become shallower. An increase in DOC may hence cause a declined autotrophic net primary production (Karlsson et al., 2009) and a reduction in the abundance and diversity of invertebrates as habitats and food types decrease. The relationship between light penetration and DOC is such that we would experience the biggest shifts in the photic zone in the sublittoral of boreal lakes. In addition, an increase in DOC could lead to a decline in DO and less favourable conditions for the fauna in the sublittoral. This is mainly because the chemocline will ascend and because the oxygen demand increases as the concentration of DOC increases (Wetzel, 2001). Similar processes may have occurred in the sublittoral elsewhere where the DOC has increased (Stendera and Johnson, 2008).

### 4.3 Relationship between environmental variables and species diversity

It is not straightforward to reach conclusions on the causes of the observed biodiversity increase. Worldwide, the biodiversity of freshwaters is declining (Sala et al., 2000). This decline is mostly caused by human impact, such as over-exploitation, water pollution, eutrophication, habitat degradation, species invasion and flow modification (Dudgeon et al., 2006). Such impacts may also lead to water shortages (Sala et al., 2005). These threats are unlikely to be acute at the sites we have studied, suggesting that other environmental variables have influenced the observed trends in species diversity. There are at least two environmental cues that potentially have changed in the study sites during the last 30 years; the deposition of long-range pollution has decreased (Monteith et al., 2007; Stoddard et al., 1999) and temperature has increased (EEA, 2012). Both can potentially influence biodiversity, either directly or indirectly.

According to our results, parts of the increased biodiversity can be attributed to a decrease in longrange pollution. This result emerges even from the spot- measurements of water chemistry in the study. The relationship would perhaps be more clear if continuous records of chemistry, or averages, were used. The relationship would clearly be more significant if the measurements were performed at the critical window of time over which the chemistry is influencing the biota. Many organisms cannot cope with low pH conditions (Raddum and Fjellheim, 1995; Raddum and Skjelkvale, 2001). When the pH lies outside the range tolerated by acid- sensitive taxa, they survive in refuges that are less influenced by acidification. As conditions improve, the sensitive taxa re-appear from the source populations. Such taxa form the basis for acidification indices and scores from these indices are now suggesting improved conditions in catchments from The Czech Republic, Germany, Norway, Sweden, UK and elsewhere (Angeler and Johnson, 2012; Hesthagen et al., 2011; Monteith et al., 2005; Murphy et al., in press).

In line with a decreased impact from long-range pollution, sulphate was the variable that was most significantly correlated with species diversity in the present study. The diversity at about one third of the riverine sites was significantly correlated with the concentration of sulphate. The concentration of sulphate in most sites in the present study varies from 1 to $20 \mathrm{mg} / \mathrm{l}$, with the exceptions of two German rivers (Ettelsbach and Heidebach) and one Latvian river (Leila Jugla), with average concentrations above $165 \mathrm{mg} / \mathrm{l}$ and $40 \mathrm{mg} / \mathrm{l}$, respectively. Sulphate is non-toxic at low concentrations, and its apparent importance in our analyses points to indirect effects on species diversity. It is not straightforward to separate collinear variables, such as pH , ANC, from the influence of sulphate. These variables are all associated with species diversity in the present study. Surrogate processes linked to sulphate may include the effects of a lowered pH that can influence the survival of aquatic insects directly, e.g., through the increase in hydrogen that interferes with the uptake and regulation of sodium and other ions (Havas and Rosseland, 1995; Paradise and Dunson, 1997), and indirectly, e.g., through aluminium toxicity (e.g., Havas and Rosseland, 1995; Sparling and Lowe, 1996).

There is increased species diversity at the Latvian sites. However, the chemistry of the Latvian rivers stands out compared to the other rivers in the study. The Latvian rivers have not experienced
acidification, and have high concentrations of copper, phosphorous and nitrogen. This suggests that the drivers of species diversity are different in Latvia compared to the other study sites. Either, the strong decreasing sulphate concentration has had a direct impact on biodiversity there, or the observed decrease in nitrogen-load has had a positive impact on the diversity.

We have not investigated the influence of temperature on species diversity. In order to do this, temperature means are needed for each site at the time of sampling, e.g., by using reanalysis approaches (http://www.ecmwf.int/research/era/do/get/index). This is an obvious next step, even though the air temperatures did not change significantly between 1990 and 2004 for many of the sites (supplementary information in Monteith et al., 2007). The influence of temperature change on species diversity is poorly understood and a simple correlation should not be expected (Walther et al., 2002). Factors affecting species distribution interact in complex ways and may influence any species directly or indirectly (Heller and Zavaleta, 2009; Mantyka-pringle et al., 2012). Species may disappear from parts of their original range and colonize new areas when the climate changes (Walther et al., 2002). In the case of rapid climate changes, not all species will be able to colonize new areas in sufficient time. Some studies report positive effects from climate change (e.g., Peterson et al., 2008), although, the general view is that climate change will cause major species extinctions (Bellard et al., 2012; Pereira et al., 2010; Thomas et al., 2004; Thuiller, 2007; Willis and Bhagwat, 2009).

### 4.4 Relationship between indices of species diversity and acidification

For some of the regions in the present study, such as Norway, the species diversity has not increased significantly in either lakes or rivers, despite a marked reappearance of sensitive taxa (Hesthagen et al., 2011; Moe et al., 2010; Raddum and Fjellheim, 1995) and despite a significant community response to temporal changes in water chemistry (Halvorsen et al., 2002; Halvorsen et al., 2003). When sensitive taxa re-appear, the acidification index will improve. The non-significant species diversity change at these sites suggests that a linear relationship between acidification indices and diversity indices should not be expected.

Acidification indices are based on the presence and abundance of acid-sensitive taxa in a sample, while species diversity indices are based on the presence and abundance of all taxa in a sample. At least three situations may induce shifts in acidification indices while the diversity indices remain more or less stable. (1) If the pre-disturbance community did not include sensitive taxa, then the acidification and the recovery did not necessarily lead to altered diversity. (2) In nature, the sensitive taxa and the tolerant taxa may interact by predation and competition causing unknown effects on diversity. For example, a sensitive species that re-appear and flourish may displace a tolerant species in the competition for space, food or other resources (Layer et al., 2010; Layer et al., 2013). (3) If acidification eradicated fish populations (Hesthagen, 1986), then the absence of a top-predator may disturb the community composition. Invertebrates that are sensitive to fish predation may flourish (Appelberg et al., 1993; Schofield et al., 1988), or sensitive taxa may survive in low pH -conditions since the total stress has no exceeded a critical limit for survival.

### 4.5 Sensitivity of species diversity in rivers versus lakes

The species diversity increase in the present study is more pronounced for rivers than for lakes. Also, the relationship between water chemistry and species diversity is equivocal for lakes and more distinct for rivers. These observations are somewhat counter-intuitive since rivers are more susceptible to temporal re-acidification events that may cause a lag in biological recovery (Ormerod and Durance, 2009). The re-acidification events occur during snow-melt in spring or during periods with heavy rain when pollutants are released during a short period. The water has not yet been buffered through soils causing a lower pH (Johannessen and Henriksen, 1978). In lakes, re-acidification events are rarer since potentially acidic water is diluted with resident water and ground water.

There are at least four non-exclusive theories that may explain the observations of a more pronounced species diversity response in rivers than in lakes. Three of these theories are founded on the homogeneity of lakes compared to rivers. E.g., rivers have highly fluctuating temperatures, fluctuating water chemistry, altered stream flow and channel instability (Lods-Crozet et al., 2001). (1) Because of the homogenous lake conditions, the original biodiversity of lakes was influenced by the acidification to a smaller extent than the biodiversity in the rivers. Hence, there is less potential for a diversity recovery in lakes. (2) The homogenous conditions in lakes may suggest a delayed chemical recovery so that the main chemical- and biological recovery have yet to occur. (3) The greater susceptibility of communities in streams to episodic shocks could make them more open to re-colonization compared to communities in lakes. In lakes, acid tolerant taxa dominate and these are more difficult to dislodge from their expanded niches. In other words, the community inertia is lower in rivers causing a faster response, including re-colonization. (4) Results from the streams may be more significant than results from the lakes because a larger fraction of the biota in streams is identified to species level. Abundant benthic macroinvertebrates in streams include mayflies (Ephemerptera), stoneflies (Plecoptera) and caddisflies (Trichoptera). The majority of these groups are identified to species level. In lakes, these insects are less abundant and non-biting midges (Chironomidae) form the most abundant benthic macroinvertebrate (Armitage et al., 1995). Non-biting midges are rarely identified below family-level for monitoring purpose, with the implication that the data resolution is lower in lakes than in streams. Supporting this, the most pronounced species diversity changes of lakes were found in Sweden with significant shifts both in $\alpha$-diversity and $\beta$-diversity. Here, the data resolution is higher than in Norway and in the UK since the non-biting midges were identified to genus or species.

### 4.6 Assemblage changes over time ( $\beta$-diversity)

The $\beta$-diversity of all assemblages has changed to some extent over time, e.g. as a response to recovery from acidification and addition of acid-sensitive taxa and/ or by natural drift. Overall, the assemblage changes differ among sites and inter-annual variability is masking any directional recovery in the species composition (Figure 11). This intern-annual variability may to some extend be random noise and/ or caused by differences in weather or sampling. Only the assemblages from the littoral zone of Swedish lakes show clear and directional changes in $\beta$-diversity. Either, the littoral of Swedish lakes has undergone unique environmental changes compared to the littoral of other regions, or a high
taxonomic resolution is needed to find a clear signal. The taxonomic resolution of the Swedish lakes is higher than the resolution from elsewhere and includes identification of the species-rich family of nonbiting midges. The taxonomic resolution is comparably high in the Swedish sublittoral and profundal samples. The sublittoral shows some directional changes in $\beta$-diversity, albeit less clear than the littoral signal, while there is no signal in the Swedish profundal. The lack of changes in the profundal could be caused by the homogenous conditions at greater depth compared to shallower areas. Our observations of directional change in the Swedish sites are supported by results from Johnson and Angeler (2010) who studied the littoral biological assemblages in several Swedish lakes, including three lakes from the present study. They concluded that the assemblage composition of acidified lakes has changes more than the assemblage composition in reference. They also found that the assemblages of acidified lakes now are becoming more similar to reference lakes. A varying degree of community responses is often found in acidified rivers in Northern Europe, even within single river system (Halvorsen et al., 2002; 2003; Sandlund et al., 2010). Nonlinear patterns of community change as a response to the chemical recovery have also been obtained from lakes in Canada (Lento et al., 2008). Together, this suggests that a biological recovery from acidification rarely will include clear directional or comparable changes among sites.

## 5. Implication of findings

### 5.1 Separating what is natural

Biological recovery from acidification includes a response to the reduced load of atmospheric pollutants, where the ideal end-point is the return to a natural or pre-acidified condition. Hence, conclusive results on the recovery can only be reached if comparable pre-state data are available. Unfortunately, information on the pre-state is lacking. A major focus for research on influence from acidification will be to separate what is natural and what is caused by man (e.g. Willis and Birks, 2006). Biological systems exhibit natural inter-annual variation that seemingly occurs under stable environmental conditions. Biological systems will also change as a response to environmental conditions. A response may be pronounced if thresholds, or so-called tipping points, are reached (Sonderegger et al., 2008). Tipping points can occur naturally when important ecotones are crossed or be induced by man.

Results from the current study suggest that there is no universally consistent pattern to biological recovery from acidification. A recovery in the community composition is likely to be site-specific. There is widespread evidence that acid-tolerant taxa have re-appeared, and concomitant increases in species diversity might therefore also be expected. It has, but not uniformly. There is a net increase in diversity, but for many sites, the increase is not statistically significant. For these sites, future records are needed to find whether the increase will be significant, or should be considered as natural nonsignificant variation. Also, more analyses are needed to separate the influence of a recovery from acidification from the influence of others stressors that have changed significantly during the last 25
years, such as temperature increase, DOC increase or eutrophication (e.g., Halvorsen et al., 2003; Stendera and Johnson, 2008).

### 5.2 Extrapolation of results

The present study includes a suite of lakes and rivers from six European countries. The sites were chosen as part of national monitoring programmes. Apart from acidification, the sites have limited human impact. Results from the study sites indicate some increase in species diversity during the last 20-30 years. Especially for many rivers, this increase is statistically significant. Results acquired for these sites should, with some precaution, be of general validity for similar sites and ecosystems. This suggests that a comparable increase in species diversity should be expected in acid-sensitive lakes and rivers elsewhere that show a chemical recovery and are otherwise little influenced by human activity. This is good news since the global biodiversity is at peril (UN, 2005). However, it is important to emphasize that the observed increase in species diversity should not be confused with a global increase in the total number of species. Most likely, the diversity has increased because species have immigrated from unacidified refugiae and/or because infrequent species have become more abundant. The study does not focus on single taxa and cannot conclude on new species, or whether threatened or rare species are now more abundant.

### 5.3 Ecosystem function

The link between biodiversity and ecosystem function is poorly understood. Many freshwater ecosystem functions are important for the services provided to society, such as the ecosystem ability to decompose organic matter, filter the water, break down toxic substances, or provide environments for recreational activities and fishing. For example, in a recent study Jenkins et al. (2013) found accelerated rates of decomposition in a headwater stream following long-term amelioration of acidity. Functions in an ecosystem are maintained by its members, the species, and the functional processes are mutually interdependent. A positive correlation has been found between species diversity and the number of functions that can be maintained within an ecosystem (Maestre et al., 2012), although the link between biodiversity and ecosystem processes are somewhat controversial. A significant decrease in diversity can be expected to cause a lowering of the ecosystems resilience (Elmqvist et al., 2003) and decreased rates of ecosystem processes (Dudgeon et al., 2006; Hooper et al., 2005). In other words, one function can be driven by more than one species in an ecosystem with high species diversity, suggesting that a loss of one species rarely influence the ecosystem. The implication is that an ecosystem with high species diversity is likely to have a better buffer capacity against pathogens or negative environmental impacts, such as pH decrease or rapid climate changes. The effect of diversity loss on ecosystem multifunctionality is particularly severe in harsh environments (Jucker and Coomes, 2012), implying that it is even more important to preserve biodiversity in harsh conditions. The species diversity of most sites in the present study is increasing. This gives hope for optimism considering that the ecosystems in the study now can be expected to have a higher buffer capacity against anticipated threats, such as climate change or habitat degradation.

### 5.4 Modelling

Given the global decline in biodiversity, ecosystem management would greatly benefit from accurate modelling of species diversity as a function of environmental scenarios or as a function of invasive species. Predictions of how biological communities may respond to future environments have so far largely been based on extrapolations from experimental and/or distributional studies on a few selected species in a restricted range of habitats (Jackson et al., 2009; Wilsey et al., 2013). In the present study, there are no clear directional changes in the biological communities ( $\beta$-diversity) for the majority of the sites, even when most sites have undergone a similar chemical recovery from acidification. This suggests that it is not straightforward to model future assemblages of zoobenthos as a function of environmental scenarios. Future responses will likely be site-specific and non-directional, similar to the observed responses in the present study. These finding are also supported by paleolimnological records including sub-fossil benthic assemblages. The biological assemblages of most lakes will follow unique trajectories through time when affected by disturbance, unless crossing major ecotones, such as introduction or removal of macrophytes in the lake or vegetation in the catchment (Brodersen and Quinlan, 2006; Velle et al., 2005). That is, the variation among lakes remains larger than the variation within lakes.

When it comes to the modelling of $\alpha$ - diversity as a function of environmental variables, results from the present study are somewhat optimistic, and especially results from the rivers. The species diversity of rivers has responded to changes in water chemistry, such as sulphate, ANC and associated changes, suggesting that scenarios for water chemistry at these sites can successfully be used to model future species diversity. However, note that the relationship between water chemistry and species diversity is not evident for all sites and that a large fraction of the diversity changes are still unaccounted for. Previous studies on species diversity have reported varying degree of projected change (Pereira et al., 2010), implying large uncertainties in the model projections. Our results conform to this and also to findings by Stockdale et al. (in press) who found a good fit between model predictions and observations for biodiversity at some sites and poorer agreement for other sites. This suggests that careful site-specific model calibration is a prerequisite for successful modelling of $\alpha$-diversity.

## 6. References

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## Appendix A. Study sites

Details on the rivers included in the analyses. WGS84 North and East indicate the geographical position given as decimal degrees, the dates indicate the time interval of the biological sampling, while the biological and the chemical samples indicate the total number of samples. St. = sampling station. The Swedish lakes include separate samples from the littoral (lit.), the sublittoral (sublit.) and the profundal (prof.)

Rivers

\left.| Country | WGS84 | WGS84 | Altitude |  | Biological | Chemical |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |  |  |$\right]$


| Country | WGS84 | WGS84 | Altitude |  | Biological | Chemical |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |  |  |


| Country | WGS84 | WGS84 | Altitude |  | Biological | Chemical |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |  |  |

## Lakes

| Country | Lake name | WGS84 <br> North | WGS84 <br> East | Altitu de (m) | L.area ( $\mathrm{km}^{2}$ ) | Date from | Date to | Biologic samples | Chem. samples |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Norway | Atnsjøen | 61.885171 | 10.144376 | 701 | 4.80 | 01.04.1998 | 01.10.2010 | 26 | 26 |
|  | Bjorvatn | 58.518766 | 8.448941 | 226 | 0.28 | 01.04.1997 | 01.10.2010 | 28 | 26 |
|  | Bredtjenn | 59.113412 | 11.678199 | 190 | 0.26 | 01.04.1997 | 01.10.2010 | 28 | 13 |
|  | Dalvatn | 69.697924 | 30.357462 | 132 | 0.35 | 01.04.1997 | 01.10.2010 | 28 | 13 |
|  | Heddersvatn | 59.831720 | 8.736000 | 1136 | 1.83 | 01.04.1997 | 01.10.2010 | 28 | 15 |
|  | Kapervatn | 58.604380 | 8.039731 | 503 | 0.07 | 01.04.1997 | 01.10.2010 | 28 | 13 |
|  | Langtjern | 69.248909 | 17.415713 | 168 | 1.32 | 01.04.1997 | 01.10.2010 | 28 | 8 |
|  | Lille Hovvatn | 60.366034 | 9.730607 | 518 | 0.23 | 01.04.1997 | 01.10.2010 | 28 | 14 |
|  | Ljosvatn | 58.415959 | 6.211179 | 150 | 0.19 | 01.04.1997 | 01.10.2010 | 28 | 26 |
|  | Lomstjørni | 58.676381 | 6.081700 | 242 | 0.07 | 01.04.1997 | 01.10.2010 | 28 | 19 |
|  | Markusdalsv. | 60.895060 | 5.255795 | 96 | 1.43 | 01.04.1997 | 01.10.2010 | 28 | 26 |
|  | Nystølvatn | 61.344976 | 6.487335 | 715 | 1.25 | 01.04.1997 | 01.10.2010 | 28 | 24 |
|  | Røyravatn | 59.605410 | 9.467070 | 450 | 0.11 | 01.04.1997 | 01.10.2010 | 28 | 28 |
|  | Rondvatn | 61.896423 | 9.799177 | 1167 | 1.03 | 01.04.1997 | 01.10.2010 | 28 | 14 |
|  | Saudlandsvatn | 59.544043 | 6.024644 | 230 | 0.42 | 01.04.1997 | 01.10.2010 | 28 | 24 |
|  | Sognevatn | 58.203981 | 6.764016 | 110 | 0.14 | 01.04.1997 | 01.10.2010 | 28 | 25 |
|  | Stortjørna | 58.316398 | 7.675419 | 268 | 0.27 | 01.04.1997 | 01.10.2010 | 28 | 14 |
|  | Svartdalsvatn | 61.983599 | 10.758875 | 868 | 0.28 | 01.04.1997 | 01.10.2010 | 28 | 8 |
|  | Svartetjern | 60.835200 | 5.572140 | 302 | 0.06 | 01.04.1997 | 01.10.2010 | 28 | 21 |
|  | $\emptyset$ vre Jerpetjern | 62.278357 | 8.842000 | 1018 | 0.64 | 01.04.1997 | 01.10.2010 | 28 | 21 |
| Sweden | Brunnsjön lit. | 56.597200 | 15.728070 | 100 | 0.10 | 30.10.1986 | 25.10.2010 | 27 | 27 |
|  | Brunnsjön prof. <br> Brunnsjön <br> sublit | 56.597200 56.597200 | 15.728070 15.728070 | 100 100 | 0.10 0.10 | 30.10 .1986 24.04 .1991 | 25.10 .2010 25.10 .2010 | 34 24 | 33 24 |
|  | Fiolen lit. | 57.080435 | 14.532324 | 227 | 1.55 | 28.04.1988 | 18.10.2010 | 26 | 26 |
|  | Fiolen prof. | 57.080435 | 14.532324 | 227 | 1.55 | 28.04.1988 | 18.10.2010 | 33 | 33 |
|  | Fiolen sublit. | 57.080435 | 14.532324 | 227 | 1.55 | 19.04.1989 | 18.10.2010 | 27 | 27 |
|  | Fräcksjön lit. | 58.151381 | 12.179369 | 60 | 0.26 | 06.11.1986 | 05.11.2010 | 27 | 27 |
|  | Fräcksjön prof | 58.151381 | 12.179369 | 60 | 0.26 | 06.11.1986 | 05.11.2010 | 34 | 33 |
|  | Fräcksjön sublit | 58.151381 | 12.179369 | 60 | 0.26 | 19.04.1989 | 05.11.2010 | 28 | 28 |
|  | Härsvatten lit. Härsvatten | 58.020200 | 12.030390 | 137 | 0.18 | 29.04.1988 | 13.10.2010 | 25 | 25 |
|  | prof. <br> Härsvatten | 58.020200 | 12.030390 | 137 | 0.18 | 29.04.1988 | 13.10.2010 | 33 | 33 |
|  | sublit | 58.020200 | 12.030390 | 137 | 0.18 | 12.04.1989 | 13.10.2010 | 27 | 27 |
|  | Stensjön lit. | 61.643253 | 16.585637 | 268 | 0.53 | 23.10.1986 | 15.10.2009 | 26 | 26 |
|  | Stensjön profun | 61.643253 | 16.585637 | 268 | 0.53 | 23.10.1986 | 11.10.2010 | 34 | 33 |
|  | Stensjön sublit | 61.643253 | 16.585637 | 268 | 0.53 | 23.05.1989 | 11.10.2010 | 28 | 28 |
|  | Storasjö lit. | 56.944310 | 15.276425 | 252 | 0.35 | 28.10.1986 | 20.10.2010 | 26 | 26 |
|  | Storasjö profun | 56.944310 | 15.276425 | 252 | 0.35 | 28.10.1986 | 20.10.2010 | 31 | 17 |
|  | Storasjö sublit | 56.944310 | 15.276425 | 252 | 0.35 | 10.04.1991 | 02.10.1995 | 7 | 7 |
|  | Tväringen lit. | 62.241186 | 15.694044 | 308 | 1.61 | 10.08.1988 | 13.10.2010 | 22 | 22 |
|  | Tväringen | 62.241186 | 15.694044 | 308 | 1.61 | 10.08.1988 | 15.10.2010 | 29 | 13 |


| Country | Lake name | WGS84 <br> North | WGS84 <br> East | Altitu <br> de $(\mathbf{m})$ | L.area <br> $\mathbf{( k m}^{\mathbf{2})}$ | Date from | Date to | Biologic <br> samples | Chem. <br> samples |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  | profun |  |  |  |  |  |  |  |  |
|  | Tväringen sublit | 62.241186 | 15.694044 | 308 | 1.61 | 17.05 .1989 | 15.10 .2010 | 14 | 14 |
| UK | Coire nan Arr | 57.417136 | -5.651864 | 125 | 0.12 | 11.04 .1988 | 08.05 .2007 | 20 | 20 |
|  | Lochnagar | 56.958266 | -3.231570 | 785 | 0.10 | 13.04 .1988 | 08.05 .2010 | 23 | 23 |
|  | Round Loch of |  |  |  |  |  |  |  |  |
|  | Glenhead | 55.093738 | -4.430448 | 295 | 0.13 | 08.04 .1988 | 04.05 .2010 | 22 | 22 |
|  | Scoat Tarn | 54.481952 | -3.299546 | 602 | 0.05 | 07.04 .1988 | 08.04 .2010 | 22 | 22 |
|  | Llyn Llagi | 53.014902 | -4.015300 | 380 | 0.06 | 22.04 .1988 | 17.04 .2010 | 23 | 23 |
|  | Blue Lough | 54.427931 | -5.955019 | 340 | 0.02 | 13.04 .1989 | 06.05 .2009 | 22 | 20 |

## Appendix B. - Taxonomic consistency

Taxa with inconsistent taxonomy through time. These were merged to the coarsest taxonomic unit. Some additional taxa were merged because of misspellings or inconsistent nomenclature (taxa not shown here).

## Norway lakes

- Diura nanseni + Diura sp.
- Halesus radiatus + Halesus sp.
- Leptophlebia marginata + Leptophlebia sp + Leptoplebia vespertina
- Limnephilidae ind + Limnephilus centralis + Limnephilus marmoratus + Limnephilus rhombicus + Limnephilus sp + Limnephilus sparsus
- Nemoura avicularis + Nemoura cinerea + Nemoura sp
- Siphlonurus aestivalis + Siphlonurus alternatus + Siphlonurus lacustris + Siphlonurus sp


## Sweden lakes

- Micronecta sp. + Micronecta poweri.
- Stictochironomus sp. + Stictochironomus rosenschoeldi
- Dicrotendipes sp. + D.modestus
- Polypedilum sp. + Polypedilum laetum gr. + Polypedilum breviantennatum gr.
- Tanypodinaae sp. + Ablabesmyia longistyla + Ablabesmyia monilis + Ablabesmyia phatta + Ablabesmyia sp.+ Conchapelopia sp + Krenopelopia sp. + Macropelopia sp. + Paramerina sp. + Pentaneurini + Procladius sp. + Thienemannimyia
- Theromyzon sp. + Theromyzon tessulatum
- Tubifex tubifex + Tub. without h.setae + Tub. with h.setae + Naididae+Limnodrilus
- Chaoborus sp. + Chaoborus obscuripes + Chaoborus flavicans + Chaoborus crystallinus
- Lephtophlebia sp. + Leptophlebia vespertina+ Leptophlebia marginata


## UK lakes

- Mystacides azurea + Mystacides sp.
- Capnia atra + Capnia sp.
- Plectrocnemia conspersa + Plectrocnemia sp.
- Tipula sp. + TIPULIDAE
- Paraleptophelia (misspelled!) + LEPTOPHLEBIIDAE
- Athripsodes aterrimus + Athripsodes sp.
- Cyrnus flavidus + Cyrnus sp. + Cyrnus trimaculatus
- Halesus radiates + Halesus sp.
- Polycentropus flavomaculatus + Polycentropus sp.
- Limnephilidae sp. + Limnephilidae. sp.


## German rivers

- Agapetus + Agapetus fuscipes + Agapetus nimbulus
- Amphinemura + Amphinemura borealis + Amphinemura standfussi + Amphinemura sulcicollis
- Chironomidae + Chironomini + Chironomus sp. + Corynoneura + Diamesa + Heterotrissocladius + Macropelopia + Orthocladiinae + Prodiamesa olivacea + Rheotanytarsus + Tanypodinae + Tanytarsini sp. + Pseudodiamesa branickii
- Brachyptera + Brachyptera risi + Brachyptera seticornis + Brachyptera starmachi
- Capnia + Capnia nigra + Capnia vidua
- Lumbriculidae + Lumbriculus variegatus + Stylodrilus heringianus + Tubifex + Tubificidae + Nais + Naididae + Limnodrilus
- Plectrocnemia + Plectrocnemia conspersa + Plectrocnemia geniculate
- Siphonoperla + Siphonoperla torrentium
- Simuliidae + Simulium + Simulium (Boophthora) erythrocephalum + Simulium (Eusimulium) angustipes + Simulium (Eusimulium) aureum + Simulium (Nevermannia) brevidens + Simulium (Nevermannia) carpathicum + Simulium (Nevermannia) cryophilum + Simulium (Nevermannia) latigonium + Simulium (Nevermannia) lundstromi + Simulium (Nevermannia) natural + Simulium (Nevermannia) urbanum + Simulium (Nevermannia) vernum + Simulium (Wilhelmia) equinum + Simulium argyreatum + Simulium monticola + Simulium noelleri + Simulium ornatum + Simulium reptans + Simulium trifasciatum + Simulium tuberosum + Simulium variegatum Gruppe
- Protonemura + Protonemura auberti + Protonemura austriaca + Protonemura intricate + Protonemura lateralis + Protonemura meyeri + Protonemura Montana + Protonemura nimborum + Protonemura nitida + Protonemura praecox


## Latvia

- Baetis niger + Baetis rhodani + Baetis
- Atherix ibis + Atherix sp.
- Halesus digitatus + Halesus interpunctata + Halesus radiates + Halesus sp.


## Norway rivers

- Agabus sp. + Agapetus sp. + Coleoptera indet. + Berosus sp. + Deronectes latus + Dytiscidae indet. + Elmidae indet. + Elmis aenea + Elodes sp. + Haliplus sp. + Helophorus sp. + Hydraena sp. + Hydraena gracilis + Hydroporus sp. + Limnius volckmari + Nebrioporus assimilis + Nebrioporus depressus + Oulimnius tuberculatus + Platambus maculatus + Stictotarsus multilineatus


## Czech Republic

- Simuliidae sp. + Simulium sp. + Simulium cf. cryophilum


## Sweden rivers

No changes

## UK rivers

No changes

## Appendix C. - Diversity details

The figures below give some details on the biodiversity (effective number of species, N1) of rivers and lakes included in the analyses. Figures in left column show raw biodiversity and figures on the right display GAM fitted to the biodiversity data. Lowermost figure shows $\beta$-diversity analysed by nonmetric multidimensional scaling (NMDS) in countries missing from Figure 11. The trajectories (lines) show assemblage changes from the 1980s and towards the present. Closely placed samples have a similar species composition.

## $\alpha$-diversity of rivers













## $\alpha$-diversity of lakes









## $\beta$-diversity of the sites that are not shown in main text



# Appendix D. Reports and publications from ICP Waters 

All reports from the ICP Waters programme from 2000 up to present are listed below. Reports before year 2000 can be listed on request. All reports are available from the Programme Centre. Reports and recent publications are also accessible through the ICP Waters website; http://www.icp-waters.no/

Escuedero-Oñate, C. Intercomparison 1327: pH, Conductivity, Alkalinity, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, $\mathrm{Mn}, \mathrm{Cd}, \mathrm{Pb}, \mathrm{Cu}, \mathrm{Ni}$ and Zn . ICP Waters Report 116/2013
Holen, S., R.F. Wright, I. Seifert. 2013. - Effects of long-range transported air pollution (LTRAP) on freshwater ecosystem services. ICP Waters Report 115/2013
Velle, G., Telford, R.J., Curtis, C., Eriksson, L., Fjellheim, A., Frolova, M., Fölster J., Grudule N., Halvorsen G.A., Hildrew A., Hoffmann A., Indriksone I., Kamasová L., Kopáček J., Orton S., Krám P., Monteith D.T., Senoo T., Shilland E.M., Stuchlík E., Wiklund M.L., de Wit, H., Skjelkvaale B.L. 2013. Biodiversity in freshwaters. Temporal trends and response to water chemistry. ICP Waters Report 114/2013
Fjellheim, A., Johannessen, A. and Landås, T.S. 2013. Biological intercalibration: Invertebrates 1612. ICP Waters Report 113/2013
Skjelkvåle, B.L., Wathne, B.M., de Wit, H. and Michela Rogora (eds.) 2013. Proceedings of the $28^{\text {th }}$ Task Force meeting of the ICP Waters Programme in Verbania Pallanza, Italy, October 8 - 10, 2012. ICP Waters Report 112/2013
Dahl, I. 2012. Intercomparison 1226: pH, Conductivity, Alkalinity, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, Cd, $\mathrm{Pb}, \mathrm{Cu}, \mathrm{Ni}$ and Zn . ICP Waters report 111/2012
Skjelkvåle, B.L., Wathne B. M. and Moiseenko, T. (eds.) 2010. Proceedings of the $27^{\text {th }}$ meeting of the ICP Waters Programme Task Force in Sochi, Russia, October 19 - 21, 2011. ICP Waters report 110/2012
Fjellheim, A., Johannessen, A., Svanevik Landås, T. 2011. Biological intercalibration: Invertebrates 1511. NIVA-report SNO 6264-2011,ICP Waters report 109/2011.

Wright, R.F., Helliwell, R., Hruska, J,. Larssen, T., Rogora, M., Rzychoń, D., Skjelkvåle, B.L. and Worsztynowicz, A. 2011. Impacts of Air Pollution on Freshwater Acidification under Future Emission Reduction Scenarios; ICP Waters contribution to WGE report. NIVA-report SNO 6243-2011. ICP Waters report 108/2011.
Dahl, I and Hagebø, E. 2011. Intercomparison 1125: pH, Cond, HCO3, NO3-N, Cl, SO4, Ca, Mg, Na, K, TOC, Al, Fe, Mn, $\mathrm{Cd}, \mathrm{Pb}, \mathrm{Cu}, \mathrm{Ni}$, and Zn . NIVA-report SNO 6222-2011. ICP Waters report 107/2011.
Skjelkvåle B.L. and de Wit, H. (Eds). 2011. Trends in precipitation chemistry, surface water chemistry and aquatic biota in acidified areas in Europe and North America from 1990 to 2008. NIVA-report SNO 6218-2011 ICP Waters report 106/2011.

ICP Waters Programme Centre 2010. ICP Waters Programme manual. NIVA SNO 6074-2010.ICP Waters report 105/2010. 91 s. ISBN 978-82-577-5953-7,
Skjelkvåle, B.L., Wathne B. M. and Vuorenmaa J. (eds.) 2010. Proceedings of the $26^{\text {th }}$ meeting of the ICP Waters Programme Task Force in Helsinki, Finland, October 4 - 6, 2010. ICP Waters report 104/2010
Fjellheim, A. 2010. Biological intercalibration: Invertebrates 1410. NIVA-report SNO 6087-2010, ICP Waters report 103/2010.

Hovind, H. 2010. Intercomparison 1024: pH, Cond, $\mathrm{HCO}_{3}, \mathrm{NO}_{3}-\mathrm{N}, \mathrm{Cl}, \mathrm{SO}_{4}, \mathrm{Ca}, \mathrm{Mg}, \mathrm{Na}, \mathrm{K}, \mathrm{TOC}, \mathrm{Al}, \mathrm{Fe}, \mathrm{Mn}, \mathrm{Cd}, \mathrm{Pb}, \mathrm{Cu}$, Ni, and Zn. NIVA-report SNO 6029-2010. ICP Waters report 102/2010.
De Wit, H. A. and Lindholm M., 2010. Nutrient enrichment effects of atmospheric N deposition on biology in oligotrophic surface waters - a review. NIVA-report SNO 6007-2010. ICP Waters report 101/2010
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